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Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups

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By changing habitat conditions, ecosystem engineers increase niche diversity and have profound effects on the distribution and abundances of other organisms. Although many ecosystems contain several engineering species, it is still unclear how the coexistence of multiple engineers affects the physical habitat and the structure of the community on a landscape scale. Here, we investigated through a large-scale field manipulation how three coexisting engineers on intertidal flats (cockles *Cerastoderma edule*; lugworms *Arenicola marina*; blue mussels *Mytilus edulis*) influence the functional composition of the local macrobenthic community and what the consequences are at the landscape level. By using biological trait analysis (BTA), we show that on the local scale biogenic changes in sediment accumulation and organic matter content translated into specific shifts in the distribution of functional traits within the community. At a landscape scale, the co-occurrence of multiple ecosystem engineers resulted in the spatial separation of different functional groups, i.e. different functional groups dominated unique complementary habitats. Our results emphasize the role of co-occurring multiple engineers in shaping natural communities, thus contributing to a better knowledge of community assembly rules. This understanding can profitably be used to improve ecosystem-based management and conservation actions.

Ecosystem engineers are organisms that have profound effects on the environment and the associated communities (Jones et al. 1994, Hastings et al. 2007, Olff et al. 2009). By modifying abiotic conditions, ecosystem engineers alter the variety of ecological niches available to other species, thus facilitating certain species and inhibiting others (Bruno et al. 2003, van Wesenbeeck et al. 2007). At the spatial scale of the engineered habitat, ecosystem engineering typically causes a shift in the community composition, which, depending on the engineer and the local conditions, may either increase or decrease community diversity (Crooks 2002). At a landscape level, however, ecosystem engineering typically enhances environmental heterogeneity, thereby increasing niche opportunities and eventually the diversity of the community (Jones et al. 1997, Wright et al. 2002, Erwin 2005).

Many natural ecosystems host several engineering species that coexist at different spatial scales and may interact to affect the surrounding habitat and communities. At small scales, multiple habitat-modifying organisms can form nested assemblages, where facilitation cascades boost local

diversity and abundance of organisms (Thomsen et al. 2010, Angelini et al. 2011), or can create mosaics of patches dominated by antagonistic engineering species that typically host distinct communities (Eklöf et al. 2011). At larger scales, the coexistence of multiple engineers in adjacent habitats often produces synergistic positive effects on landscape heterogeneity and biodiversity (Altieri et al. 2007), but may also have neutral or negative effects on associated communities (Micheli and Peterson 1999, Grabowski et al. 2005, Geraldi et al. 2009). Despite the prevalence of multiple engineering species in natural ecosystems, our current knowledge of the importance of their interactive effects is still limited and questions such as how the coexistence of engineers affect the physical habitat and the structure of the community on a landscape scale remain to be answered.

Here, we focus on three well-known ecosystem engineers that coexist in soft-bottom intertidal ecosystems: cockles *Cerastoderma edule*, lugworms *Arenicola marina* and blue mussels *Mytilus edulis*. We tested how the combined effect of these species altered their environment across space and how

the resulting modulated niche space affected the community composition at a landscape level. For this purpose, we set up a large-scale field experiment in which we manipulated a total of 2400 m² of intertidal mudflat by adding a total of 800 000 cockles and 64 000 lugworms to 25-m² plots either in close proximity to or far away from mussel reefs. We then examined how these multiple engineers affected the functional trait diversity of the community locally by modulating sediment properties, and how this influenced the community at a landscape scale. Functional traits of species are related to life-history attributes that are specifically selected by the environment (Bremner et al. 2006). Hence, the investigation of the community's functional composition could provide direct insights into the underlying mechanisms by which ecosystem engineers affect the surrounding habitat and community. Here, we predict that 1) different ecosystem engineers will locally promote specific shifts in biogenic habitats and community functional composition, 2) these shifts will be conditional on the interactive effects caused by other engineering species (i.e. mussels), and 3) multiple engineers together will increase habitat heterogeneity, thus favoring the spatial separation of different functional groups at a landscape scale.

Study system and methods

Study system

The field experiments were conducted on the intertidal flats south of the barrier island of Schiermonnikoog, in the Dutch Wadden Sea, one of the world's largest intertidal soft-sediment ecosystems. Here, mussels, lugworms and cockles commonly co-exist at a landscape scale. Mussels typically form large (> 1 ha) aggregations, which cause long (several hundred meters) spatial gradients in sediment composition (van der Zee et al. 2012, Donadi et al. 2013a). Lugworms occur evenly with relatively stable densities of 20–40 individuals m⁻² (Beukema and Devlas 1979), while cockles can form dense beds of up to a thousand individuals m⁻² that extend for several hundred meters (Jensen 1992, Donadi et al. unpubl.). While cockles and lugworms commonly co-occur at a small scale (< 0.1 m), they do not usually survive in the anoxic sediments within mussel aggregations.

The lugworm *Arenicola marina* is a sediment-destabilizing polychaete that promotes erosion of fine material through bioturbation and oxygenates the sediment by flushing its burrows (Rhoads and Young 1970, Levinton 1994, Volkenborn et al. 2007). In contrast, blue mussels *Mytilus edulis* typically enhance sediment organic matter and silt content at large spatial scales by forming dense aggregations that provide shelter from tidal currents (Donadi et al. 2013a) and produce large amount of faeces and pseudofaeces (Kröncke 1996). The filter-feeding cockle *Cerastoderma edule* has been previously described as a bioturbator (Ciutat et al. 2007, Montserrat et al. 2009). However, recent studies suggest that high densities of cockles can locally increase sediment stability through the production of mucus-rich biodeposits or protrusion of shells from the sediment (Andersen et al. 2010, Donadi et al. 2013b). Given the evidence on the effects of lugworms, mussels and cockles on their

habitat and surrounding communities (Volkenborn and Reise 2007, Ysebaert et al. 2009, this study) and their wide-spread occurrence in soft-bottom intertidal systems, these species can be considered among the main ecosystem engineers on mudflats.

Experimental treatments

To test the effects of the three engineers on both environmental conditions and the associated macrofaunal community, we created plots with cockle-dominated communities and lugworm-dominated communities in a randomized block design within the pseudofaeces plumes of two mussel beds at a distance of 100 and 350 m from the reefs, respectively (53°28'8.15"N, 6°13'27.95"E; 53°28'2.44"N, 6°10'59.83"E) and at two, unaffected sandy sites without mussel beds at the same tidal elevation, respectively (53°28'7.42"N, 6°13'55.95"E; 53°28'7.54"N, 6°11'33.48"E). In two previous papers we have shown that differences in sediment composition between mussel bed sites and sandy sites are caused by engineering effects of the mussel reefs, which increase sediment organic matter and silt content through biodeposition and hydrodynamic stress alleviation (van der Zee et al. 2012, Donadi et al. 2013a). Each site was assigned two blocks of twelve 5 × 5 m plots for a total of 96 plots. In June 2010, one-third of the plots was enriched with high densities of cockles (1000 individuals m⁻²), one-third with high densities of lugworms (80 individuals m⁻²) and the remaining plots served as a control (no addition; Supplementary material Appendix 1). Treatment densities of cockles and lugworms were chosen to mimic naturally occurring communities dominated by either species (Beukema 1979). Cockles were collected by fishermen from a nearby intertidal flat and were two to four years old. Lugworms were harvested by a commercial lugworm fisheries company from an intertidal flat in the western Wadden Sea.

Abundance of transplanted specimens was monitored every six months within 0.5 × 0.5 m frames placed on the experimental plots. The number of lugworm fecal casts, which is a good proxy for worm density (Eklöf et al. 2011), was visually estimated within three frames per plot. Cockles were counted by gently sieving the surface sediments by hand. Field observations showed no effects of sediment disturbance on sediment organic matter content and pore water redox potential 24 h after counting cockles (Donadi et al. unpubl.). However, to minimize disturbance, only one frame was used to estimate cockle density in each experimental plot. Abundances of both cockles and lugworms generally decreased after the transplantations but remained considerably higher in enriched plots compared to the other treatments. The only exception was lugworm abundance at the end of the experiment in September 2011; at this time there was no difference between cockle and lugworm-addition plots (Supplementary material Appendix 2).

Field sampling and laboratory analyses

Macrofauna

In September 2011 (16 months after the start of the experiments), one sediment core (diameter = 15 cm) was extracted

from the center of each plot to a depth of 20–25 cm, corresponding to the depth of a compact layer of shell debris underneath which no macrobenthic organisms were found (Donadi et al. unpubl.). Sediment cores were sieved over a 1 mm mesh and macrofauna were fixed in 10% formalin and stained with Rose Bengal Red. All organisms were identified (mostly to species level) under a 10× magnification stereo microscope and the dry biomass (shell-free dry mass) of each taxon was measured after drying for 48 h in an oven at 60°C. In total we collected 14084 individuals belonging to 29 taxa.

Sediment properties

Sediment samples were collected from each plot in September 2011 through cut disposable syringes (diameter = 2.4 cm, depth = 0–5 cm). Organic matter content was estimated from oven-dried (48 h, 75°C) samples as loss on ignition (LOI; 4 h, 550°C) and silt content (fraction < 63 µm) was measured with a Malvern particle size analyzer after freeze-drying the sediment samples. Percentages of organic matter and silt content measured at the end of the experiments (September 2011) were used for data analyses. Elevation of plots (bed level height) was measured in March 2010 and September 2011 using a precision laser. At each site, measurements were calibrated against fixed reference metal poles. Five replicates per plot were collected and averaged, and the differences between the two dates were used to estimate bed level changes over the course of the summer, when bioengineering activity of cockles and lugworms is most conspicuous. Positive values of bed level changes indicate net sediment accumulation, while negative values indicate net sediment erosion.

Data analysis

We applied biological trait analysis (BTA) to detect changes in the pattern of trait expression caused by the engineering effect of cockles, lugworms and mussels. BTA uses life history, behavioral and morphological characteristics of the species to describe the ecological functioning of an assemblage (Bremner et al. 2006). Five biological traits, i.e. 'body size', 'living depth', 'feeding mode', 'bioturbation' and 'longevity', were selected, and each trait was divided into several categories following Jones and Frid (2009) (Table 1). Individual taxa were scored for the extent to which they display the trait category using a 'fuzzy coding' procedure (Chevenet et al. 1994); this allowed taxa to exhibit trait categories to different degrees. Taxa were scored from 0 to 3, with 0 indicating no affinity and 3 indicating total affinity to a trait category (Supplementary material Appendix 3). When trait information for a taxon could not be obtained (in only 3% of cases), 0 scores were used and thus did not influence the analysis (Chevenet et al. 1994). Fuzzy scores were standardized in such a way that within each trait, the category scores for each taxon summed to 1. Information on biological traits was obtained from published peer-reviewed literature and online databases for European marine invertebrates. *Cerastoderma edule* and *Arenicola marina* were excluded from the analysis, as they were experimentally manipulated.

Trait category scores of each taxon were multiplied by the biomass of the taxon for every sample and subsequently

Table 1. Functional traits and categories used in the fuzzy coding of taxa (adapted from Jones and Frid 2009).

Trait	Category	Abbreviation
Bioturbation	none	none
	biodiffuser	biodif
	fauna that move sediment in a random manner causing diffusive mixing (François et al. 1997)	
	gallery diffuser	gall
	fauna that build extensive galleries of burrows that are irrigated by biotic activities (François et al. 2002)	
	upward-conveyor	upw
	head-down oriented fauna that cause active movement of sediment from depth to the surface (François et al. 1997)	
Depth	downward-conveyor	down
	Head-up oriented fauna that cause active movement of sediment from the surface to depth through their gut (François et al. 1997)	
	bio-irrigator	bioirr
	fauna which actively irrigate burrows by drawing down surface water past their gills (Jones and Frid 2009)	
	surface	surf
	0–3 cm	d0_3
	3–8 cm	d3_8
Body size (mm)	8–15 cm	d8_15
	15–25 cm	d15_25
	> 25 cm	d > 25
	< 5	s < 5
	5 < > 10	s5_10
	10 < > 20	s10_20
	20 < > 40	s20_40
Feeding mode	40 < > 80	s40_80
	> 80	s > 80
	deposit feeder	dep
	suspension feeder	susp
	opportunistic/scavenger	opp
	grazer	graz
	predator	pred
Longevity	< 1 year	< 1y
	1–2 years	1_2y
	3–5 years	3_5y
	6–10 years	6_10y
	> 10 years	> 10y

summed across all taxa to provide a sample-by-trait matrix containing a total score for each functional category and for each sample. This sample-by-trait matrix, containing a total of 96 samples and 28 trait categories, was analyzed using principal component analyses (PCA) in Canoco for Windows ver. 4.55 (ter Braak and Smilauer 2002). Gradient lengths were first estimated in a detrended correspondence analysis (DCA). As the lengths of DCA axes 1 and 2 were both lower than 3, we used PCA, which assumes linear responses of species to environmental gradients (ter Braak and Smilauer 2002). Matrix data were square-root transformed

prior to ordination to reduce skewness. Adjusted species scores, which are the regression coefficients of the standardized species data on the sample scores (ter Braak and Smilauer 2002), indicated affinity of PC axes to different trait categories.

To explore whether cockles, lugworms and mussels interactively affected the community structure and environmental conditions, a linear mixed-model including the fixed factors 'engineer addition' (three levels: cockle addition, lugworm addition, no addition), 'habitat' (two levels: sandy sites, mussel bed sites) and their interaction was used to explain variation in the sample scores of the first and second principal component axis, and in the values of sediment organic matter and silt content and bed level change. A two-nested random-effect structure, taking into account sites (four levels) and blocks (eight levels) within a site, significantly improved the model fit, as indicated by AIC values and likelihood ratio tests, after p-values were corrected for testing on the boundary (Zuur et al. 2009). To account for heteroscedasticity, a residual variance structure was included in the models (Zuur et al. 2009). Comparisons based on AIC values indicated that the best models were those in which the variance was allowed to differ between sites. Significant treatment effects were assessed through a stepwise backward elimination method, where likelihood ratio tests are used to compare full models to reduced models where each factor is dropped at a time (Zuur et al. 2009). Marginal and conditional R^2 , which describe the proportion of variance explained by the fixed factor alone and by both the fixed and random factors, respectively, were calculated according to Nakagawa and Schielzeth (2013). Independence, normality and homogeneity of variance of residuals were confirmed by plotting relationships between residuals vs random factors and fitted values, and observed vs theoretical quantiles (QQ-plots). When either fixed factors or their interaction was found significant, multiple comparisons were performed and the familywise error rate was controlled with the Bonferroni correction.

To explore overall effects of engineers on the large-scale structure of the community, values of organic matter content and elevation change for each plot were weighted by the scores of the functional categories to give weighted averages for each functional category. Weighted averages therefore indicated sediment conditions at which each category was observed most frequently. Standard error of weighted averages were calculated following Cochran (1977), as suggested by Gatz and Smith (1995). All statistical calculations except multivariate analyses were carried out in R 2010 (<www.r-project.org/>).

Results

Local effects on sediment properties

Effects of cockles and lugworms on sediment organic matter content were conditional on the proximity of the mussel beds (interaction effect between Engineer addition and Habitat, Table 2, Fig. 1A). Coastward of mussel beds both cockles and lugworms decreased percentage of organic matter compared to no-addition plots (post hoc test, $p = 0.002$ and $p < 0.001$, respectively), while at the sandy sites a significant reduction was observed only in lugworm-addition plots relative to no-addition plots (post hoc test, $p < 0.001$; Fig. 1A). Overall, organic matter content was 3 times higher and showed larger variation between blocks close to the mussel beds than at the sandy sites (post hoc test, $p = 0.017$; Fig. 1A).

Silt content was 3.5 times higher coastward of mussel beds than on sand (main effect of Habitat, Table 2, Fig. 1B), and was significantly decreased by cockles and lugworms compared to no-addition treatment (main effect of Engineer addition, Table 2; post hoc test, $p = 0.004$ and $p < 0.001$, respectively; Fig. 1B). As for organic matter content, the variation between blocks in the mussel bed sites was larger than at the sandy sites, likely due to particularly high values coastward of one of the mussel beds.

Elevation measurements indicated that cockles induced sediment accumulation (main effect of Engineer addition, Table 2, Fig. 1C). There was no interaction effect between Engineer addition and Habitat, as the effect was consistent in all but one block close to the mussel beds, where there was no difference between treatments. Elevation in the cockle-addition plots increased by on average 1.41 ± 0.23 cm (mean \pm SE; $n = 32$) over the summer (March–September 2011), whereas elevation in no-addition and lugworm-addition plots increased only by on average 0.29 ± 0.11 cm (mean \pm SE; $n = 32$) and 0.30 ± 0.15 cm (mean \pm SE; $n = 32$), respectively.

Local effects on macrofauna

Cockles and lugworms had specific effects on the functional trait distribution of the macrofauna, which depended on the proximity to the mussel beds (Fig. 2A–B). The first two PCA axes explained 66% of the total variance, with 40% of variance across principal component axis 1 (PC1) and 26% across axis 2 (PC2). Adjusted species scores (Table 3) indicated that PC1 displayed relatively strong positive correlations with large species (body size 20–40 mm, 40–80 mm

Table 2. Results of linear mixed-models showing effects of Engineer addition (E), Habitat (H) and their interaction (E \times H) on sediment conditions and PC scores. Only likelihood ratio test statistics (LRT) and p-values of significant factors are shown. Marginal R_m^2 and conditional R_c^2 of the models are provided.

Response	Engineer add. (E)		Habitat (H)		E \times H		R_m^2	R_c^2
	LRT	P	LRT	P	LRT	P		
Organic matter content					10.26	0.006	0.74	0.98
Silt content	26.77	<0.001	6.35	0.012			0.72	0.95
Bed level change	52.75	<0.001					0.31	0.55
PC1 scores					10.42	0.006	0.26	0.37
PC2 scores	9.07	0.011					0.04	0.21

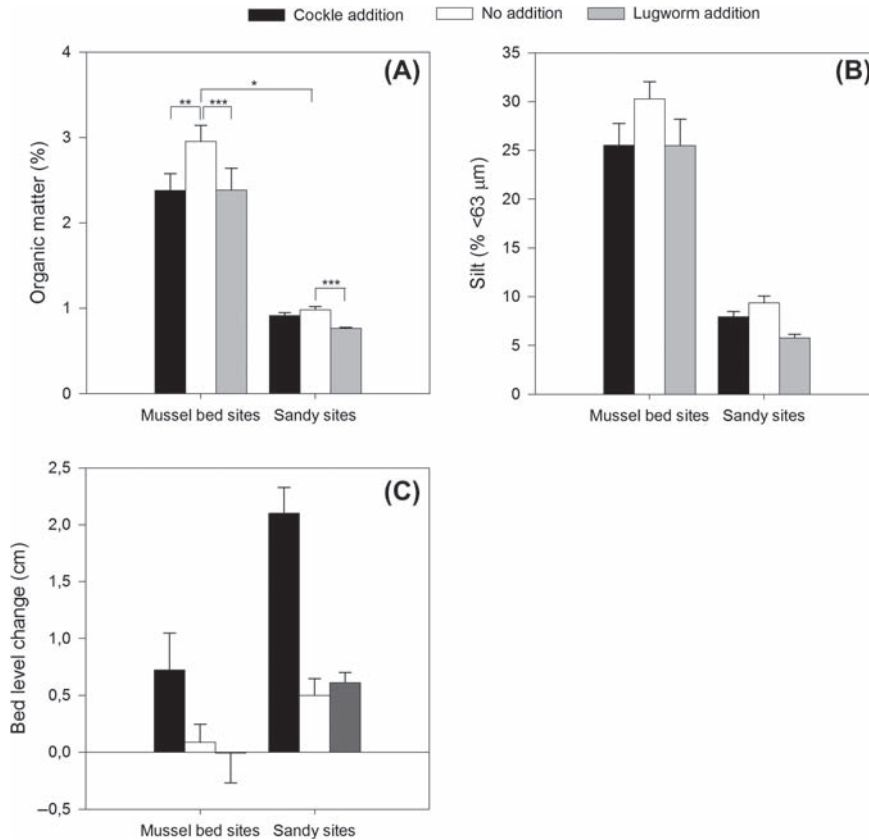


Figure 1. (A) Sediment organic matter and (B) silt content, and (C) bed level change in cockle-addition, lugworm- addition and no-addition plots in sites located coastward of mussel reefs and sandy sites without mussels. Mean \pm SE (n = 16). Post hoc analysis: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

and above 80 mm), deep-living species (depth 8–15 cm and 15–25 cm) deposit and suspension feeders. PC2 was positively correlated to small species (body size below 5 mm, 5–10 mm and 10–20 mm), shallow-living species (depth 0–3 cm and 3–8 cm) and biodiffusers, but negatively correlated to gallery diffusers and organisms with a short life-span (≤ 1 year, 1–2 years). Along PC1, cockles and lugworms had contrasting effects on the functional trait composition coastward of mussel beds, while they did not have any effects at the sandy sites (significant interaction effects between Engineer

addition and Habitat, Table 2, Fig. 2A). In the lugworm-addition plots proximal to mussel beds, PC1 scores were higher than in cockle-addition plots close to mussel beds (post hoc test, $p = 0.0207$) and lugworm-addition plots in the sandy sites (post hoc test, $p = 0.002$), which suggests that joint effect of lugworms and mussel reefs might enhance specific functional groups, such as large and deep-living species, and deposit and suspension feeders. Cockle-addition plots significantly increased PC2 scores compared to lugworm-addition plots (main effect of Engineer addition,

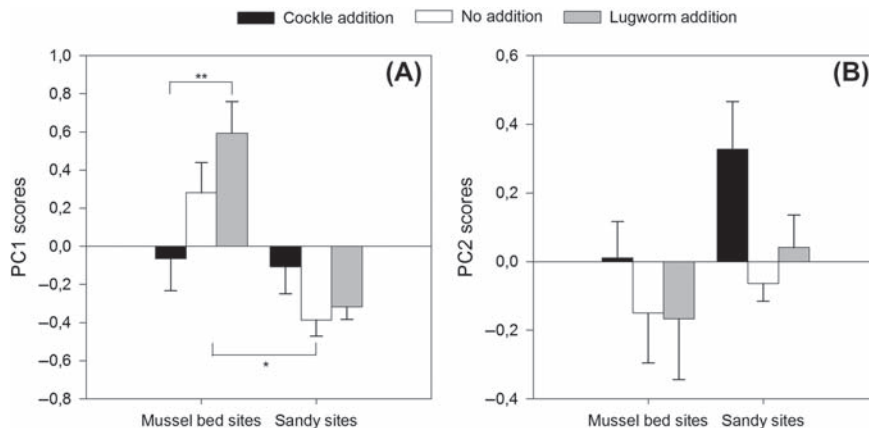


Figure 2. (A) PC1 scores and (B) PC2 scores in cockle-addition, lugworm-addition and no-addition plots in sites located coastward of mussel reefs and sandy sites without mussels. Mean \pm SE (n = 16). Post hoc analysis: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Table 3. Species scores (adjusted for species variance) for the first two principal components.

Functional category	PC1	PC2
none	0.118	0.238
biodiffuser	0.863	1.425
gallery diffuser	0.983	-1.123
upward-conveyor	-0.049	-0.361
downward-conveyor	0.007	0.177
bio-irrigator	1.007	0.474
surface	0.097	0.185
0–3 cm	0.848	1.427
3–8 cm	0.846	1.335
8–15 cm	1.270	-0.768
15–25 cm	1.103	-0.807
> 25 cm	0.329	0.377
< 5	0.676	1.031
5 < > 10	0.737	1.281
10 < > 20	0.766	1.251
20 < > 40	1.301	-0.354
40 < > 80	1.180	-0.942
> 80	1.202	-0.998
deposit-feeder	1.345	0.054
suspension-feeder	1.219	0.868
opportunistic/scavenger	0.696	-0.980
Grazer	0	0
predator	0.512	-0.731
< 1 year	0.964	-1.103
1–2 years	1.126	-1.082
3–5 years	0.748	-0.293
6–10 years	0.904	1.445
> 10 years	0.262	0.318

Table 2; post hoc test, $p = 0.019$; Fig. 2B) and no-addition plots (post hoc test, $p = 0.038$; Fig. 2B), both coastward of the mussel beds and on the sand, indicating an overall facilitative effects of cockles on small-sized organisms, shallow-living species and biodiffusers. Our results indicate that the coexistence of multiple engineers can differentially affect the functional composition of the local communities.

Landscape effects on habitat and community functional composition

At the landscape scale, the combined engineering effects of cockles, lugworms and mussels increased habitat heterogeneity and resulted in the spatial separation of functional groups of macrofauna (Fig. 3). Different functional categories dominated habitats with different sediment properties. Functional categories related to the trait ‘body size’ sorted along gradients of organic matter content and bed level change, so that small species occurred predominately at high levels of sediment accumulation and low organic matter content, while larger species preferred sediments enriched with organic matter and low sediment accumulation (Fig. 3A). Accordingly, due to collinearity among functional categories (Supplementary material Appendix 4), habitats with high rates of sediment accumulation typically hosted shallow-living species, suspension feeders, biodiffusers, and organisms with a relatively long life-span, whereas sediments enriched with organic matter were mainly inhabited by deep-living species, grazers, downward conveyors, bioirrigators, and organisms with a relatively short life-span (≤ 2 years)

(Fig. 3B–E). Our results show that changes in organic matter content and plot elevation caused by the combination of species-specific engineering effects (Fig. 3F) translated into changes in the distribution of functional traits within the macrobenthic community on a landscape scale (Fig. 3A–E).

Discussion

We found that habitat modification across multiple spatial scales by three coexisting ecosystem engineers resulted in the spatial separation of functional groups of macrobenthos on an intertidal flat. By modifying sediment organic matter content and sediment accumulation in different ways, cockles, mussels and lugworms caused specific shifts in the community functional composition on a local scale. At the landscape level, their joint effects increased habitat heterogeneity, which in turn mediated niche availability and caused different functional groups to become dominant in different complementary habitats.

Our results demonstrate that multiple engineering species contribute simultaneously to the structuring of ecosystems. Although our large-scale experiment provides a single example of such interactions, it is relevant to other systems where engineering networks might shape the ecological community through interactive effects (Davidson and Lightfoot 2006, Altieri et al. 2007, Thomsen et al. 2010). For example, in macroalgal beds, the clam *Anadara trapezia* was shown to enhance epibenthic species richness and abundance when occurring together with the alga *Caulerpa taxifolia*, which altered the clam’s burial depths (Gribben et al. 2009). On cobble beaches, a facilitation cascade between adjacent assemblages of cordgrass *Spartina alterniflora* and ribbed mussels *Geukensia demissa* increased the abundance of organisms, the diversity and overall stability of the associated communities (Altieri et al. 2007). In intertidal soft-sediment systems several studies reported on single engineering effects of cockles, lugworms and mussels (Ciutat et al. 2007, Volkenborn and Reise 2007, Ysebaert et al. 2009). However, in the real world these species coexist at various spatial scales, and our results suggest that they will act synergistically to shape the environment, and that their effects may well be conditional on the proximity of other engineering species. For example, cockles are primarily known as bioturbators that mobilize fine material from the sediment and thereby decrease sediment stability (Ciutat et al. 2007, Montserrat et al. 2009). Indeed, we found that cockles significantly reduced organic matter and silt content near the mussel beds, thus acting as sediment destabilizers. However, in sandy areas away from the influence of the reefs, cockles enhanced sediment accumulation. In a previous study we showed that such increases in elevation corresponded to an increase in critical erodibility stress, which indicates enhanced sediment stability (Donadi et al. 2013b). This illustrates the strong context-dependence of the engineering effects of cockles in our system (Donadi et al. 2014). Moreover, we found that lugworms facilitated large and deep-living species, but only near the mussel beds where the sediment was muddier. Muddy sediments are prone to anoxia, hence bioirrigation by lugworms might be essential to allow oxygen penetration in the soil (Volkenborn et al.

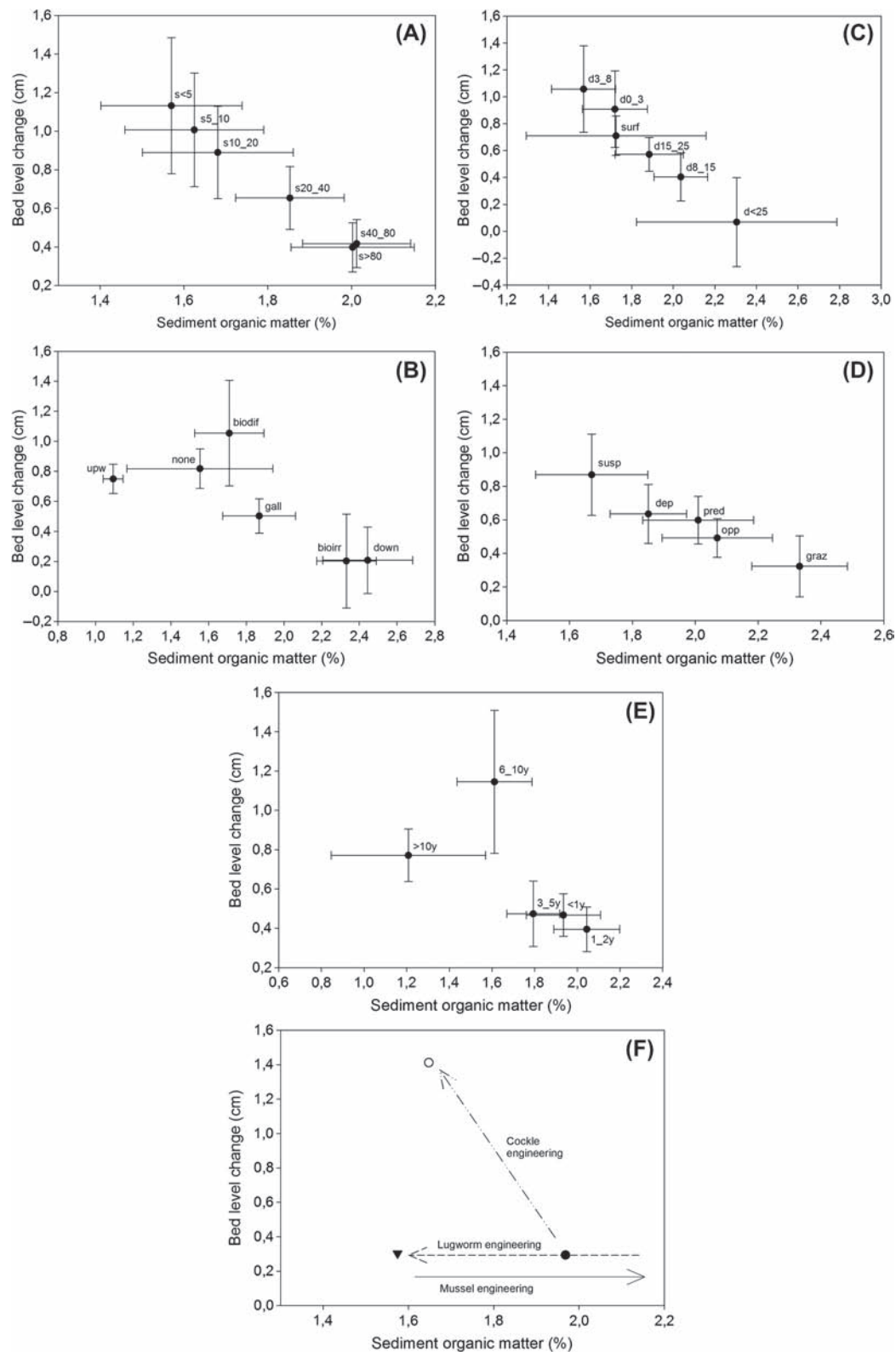


Figure 3. Different functional categories are associated to different sediment conditions determined by the joint engineering effects of cockles, lugworms and mussels. Scatter plot of weighted averages of sediment organic matter content and bed level change for each category of the functional trait (A) 'body size', (B) 'bioturbation', (C) 'depth', (D) 'feeding mode', and (E) 'longevity' (see abbreviations in Table 1). (F) Averages of organic matter content and bed level change in cockle-addition plots (white dot), lugworm-addition plots (triangle) and no-addition plots (black dot). Arrows indicate the observed main engineering effects of cockles, lugworms and mussels.

2007). Overall, our results emphasize the need for an integrative approach that incorporates parallel networks of non-trophic relationships such as ecosystem engineering into classic community ecology (Ings et al. 2009, Olff et al. 2009, Kéfi et al. 2012).

Our results demonstrate that shifts in biogenic habitats correspond to shifts in the functional composition of the community. At the conclusion of our experiment, after 18 months from the initial manipulation, we found that different traits were favored by specific changes in sediment conditions in our experimental plots. Small-sized species (e.g. the polychaetes *Aphelocheata marioni* and *Capitella capitata*, and the amphipod *Urothoe poseidonis*, Supplementary material Appendix 3) were preferably associated with habitats characterized by higher sediment accumulation and lower organic matter content, caused by engineering effects of cockles. This suggests that cockles facilitated small-sized species by decreasing sediment erosion, which likely prevented the resuspension and transport of small organisms from the surface sediments by waves and tidal currents (Donadi et al. 2013a). In contrast, larger species, such as the bivalve *Scrobicularia plana*, the polychaetes *Hediste diversicolor* and *Lanice conchilega* (Supplementary material Appendix 3), were mainly found in sediments with high organic matter content and low sediment accumulation, and were particularly abundant in the lugworm-addition plots in the mussel bed sites. Many of these species are primarily deposit-feeders and may be favored by the large amount of biodeposits accumulated by mussels, but may also profit from the bioturbating activity of lugworms in organic-rich sediments (Kristensen et al. 2012). Alternatively, competition for space could prevent large species from settling in cockle-dominated communities. Also, the engineered habitat might have selected on functional traits other than body-size and feeding mode (de Roos and Persson 2013), such as living depth, i.e. shallow-living species could have been promoted by sediment stabilization caused by cockles. Although the precise underlying mechanism still needs to be unraveled, our study demonstrated that different biogenic habitats promoted specific functional groups in the associated communities. Such understanding not only can improve our ability to predict impacts of human activities on ecosystem engineer populations, but also suggests that the functional composition of associated communities may be used as a useful tool to monitor ecosystems state and properties (Bremner et al. 2006, Frid et al. 2008).

In marine systems, analysis of functional traits has been used to describe ecological functioning of natural assemblages (Bremner et al. 2006, Paganelli et al. 2012), assess anthropogenic impacts on the community (Tillin et al. 2006, Kenchington et al. 2007, Cesar and Frid 2009), and more recently, for monitoring and management purposes (Bremner 2008, Frid et al. 2008, van der Linden et al. 2012). Nevertheless, the application of trait-based approaches to explore ecosystem engineering effects is still uncommon (Volkenborn and Reise 2007, Cesar and Frid 2009). Our study shows that the analysis of functional traits can provide strong insights into the underlying mechanisms of facilitation and inhibition by which ecosystem engineers control the community.

In summary, we show that the joint effects of three engineering species determine the large-scale structure of an intertidal macrobenthic community. Given that ecosystem engineering is a common and an important type of biotic interactions in ecosystems worldwide, we suggest that the occurrence of engineering networks could be a rule rather than an exception. Hence, it is essential to identify the players in such networks and their net effects if we wish to understand, preserve and restore natural ecosystems.

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Supplementary material (available online as Appendix oik.02100 at <www.oikosjournal.org/readers/appendix>). Appendix 1: Diagram of the experimental design. Appendix 2: Cockle and lugworm abundances in the experimental plots over one year. Appendix 3: Fuzzy scores for each trait category and taxon. Appendix 4: Spearman correlation coefficient for each pair of functional trait categories.